5-2017

Caterpillar Growth and Consumption Rates as a Measure of Sugar Maple (Acer saccharum) and American Beech (Fagus grandifolia) Leaf Quality following an Icing Event

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by

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May 2017

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Abstract

Ice storms are predicted to increase in frequency and intensity with climate change. The impact this will have on northeastern forests is largely unknown. Increased ice storm frequency and intensity will likely change the structure and function of forested ecosystems. The consequences of this change have never before been studied in a controlled, experimental setting. The Ice Storm Experiment (ISE) at the Hubbard Brook Experimental Forest in Woodstock, New Hampshire, imitated ice storms at three levels of severity: low, moderate, and high. Leaves were collected from sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) located within the plots. Relative leaf quality was assessed with gypsy moth larvae (*Lymantria dispar* dispar) bioassays. Larvae were allowed to feed on sugar maple of American beech leaves for approximately 72 hours in an incubation chamber. Caterpillar growth rate and caterpillar consumption rate were calculated to assess relative leaf quality. Growth rate was highest in the plots receiving the highest treatment of ice for both sugar maple and American beech. Consumption rate was lowest in the high treatment plots for both sugar maple and American beech. These findings suggest that leaf quality of these species is highest following a severe ice event. In the future, leaf chemical analyses will be conducted to determine the physical makeup of the leaves.

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Advice to future honors students

If you are on the fence about completing your own research and turning it into a thesis, just do it. Yes, it is a lot of work, and it can be very stressful at times, but when you graduate having that under your belt, it is going to set you apart by a long shot. Pick a topic you are passionate about and pour everything you have into it. Many undergraduates never have the opportunity to conduct independent research; do not take it for granted. Finally, do not wait until the last possible week to submit your thesis. However, if you do, know that everything will probably turn out all right anyways. Take a deep breath. You can do this.

Acknowledgments

First and foremost, I would like to thank Wendy Leuenberger for her patience, teaching, and guidance throughout the duration of this project. None of this could have happened without her. I would also like to thank Lindsey Rustad, John Campbell, and Charles Driscoll for providing me with the opportunity to conduct research, as well as guidance and support. Thank you to Seaira Goetz and numerous other laboratory staff and volunteers for their many hours spent processing data in Illick Hall during the hot summer months. Finally, I would like to thank my advisor, Dylan Parry, for guiding me through this entire process and providing me with the opportunity to go to Hubbard Brook.

Thesis Project Body

1. Introduction and Literature Review

Climate change is expected to change the frequency and intensity of natural disturbances. (Dale et al., 2001; Rustad & Campbell, 2012). Some studies have predicted that ice storms will increase in frequency and intensity in northeastern America and eastern Canada due to climate change (Dale et al., 2001; Cheng et al., 2007). The National Weather Service defines an ice storm as a precipitation event resulting in at least 6.35 mm of ice accumulation (Irland, 2000). Ice storms are extremely dangerous, and can be costly. The ice storm of January 1998 was one of the most severe ice storms seen in North America to date (Duguay et al., 2001; Weeks et al., 2009; Rustad & Campbell, 2012). The storm left 1.4 million people without power, and was responsible for 17 deaths and over $1 billion worth of damages (DeGaetano, 2000).

Sugar maple (*Acer saccharum*) trees are considered resilient to damage from ice storms (Horsley et al., 2002; Pisaric et al., 2008). De Steven et al. (1991) found that, following an ice storm in 1976, sugar maple tree density decreased slightly at the canopy level. The forest showed a general shift to the persistence of American beech (*Fagus grandifolia*) (De Steven et al., 1991). American beech, like sugar maple, is considered a very shade-tolerant species (Burns & Honkala, 1990). American beech is also considered tolerant of icing and wind (Burns & Honkala, 1990; De Steven et al., 1991).

Rhoads et al. (2002) conducted a quantitative visual assessment at the Hubbard Brook Experimental Forest in Woodstock, New Hampshire following the ice storm of 1998. Rhoads et al. (2002) concluded that beech sustained more damage than sugar maple in the canopy. The ice storm initially created an opening in the canopy (Rhoads et al., 2002; Weeks et al., 2009). Weeks et al. (2009) found increased growth and survivorship of beech saplings in plots damaged by the ice storm of 1998 than those that were undamaged. Weeks et al. (2009) also found an increase in beech tree height and size in the damaged plots.

Hirao et al. (2008) found that caterpillar (Lepidoptera) abundance increased in response to windthrow (blowdown) events. This increase in abundance may be due to improved light conditions as a result of gaps created by damaged trees (Hirao et al., 2008). Herbivorous insects, such as Lepidoptera, are more abundant in canopy gaps and large openings than under a closed canopy (Shure & Phillips, 1991; Takafumi et al., 2010). Shure and Phillips (1991) conducted their study in manmade gaps in the southern Appalachian Mountains, while Takafumi et al. (2010) studies gaps created by a typhoon disturbance in Japan. In North Carolina, Hunter & Forkner (1999) found that insect herbivore defoliation was higher in areas damaged by a hurricane than areas that were not affected. Microenvironmental factors such as predation pressure, abiotic differences, and physiological limitations can limit arthropod abundance in canopy gaps (Shure & Phillips, 1991). It is expected that disturbance caused by ice storms and the resulting plant/herbivore interactions will be similar to disturbance caused by hurricanes and other windthrow events.

Increased light conditions in canopy gaps may improve overall leaf quality, making gaps favorable to herbivorous arthropods (Hirao et al., 2008). Leaf area index (LAI), the green leaf area in relation to ground area, increases with higher photosynthetic photon flux density (%PPFD), the amount of light reaching a surface, in sugar maple and American beech seedlings (Beaudet & Messier, 1998). Leaf area ratio (LAR), the ratio of leaf dry weight to photosynthetic area, decreases with increasing %PPFD in sugar maple and American beech seedlings (Beaudet & Messier, 1998). Canham (1988) found that sugar maple sapling LAI increased in a small canopy gap. Photosynthetically active radiation (PAR), the light available for photosynthesis increases in even a small, single-tree gap in northern hardwood forests (Canham et al., 1990).

2. Hypotheses

1. *Caterpillar growth rate will be lower when fed sugar maple leaves exposed to high treatment than for medium, low and control treatments.* Icing will negatively impact canopy sugar maple trees. Sugar maple leaves in the high treatment plots will be of lower nutrient quality.

2. *Caterpillar growth rate will be higher when fed beech leaves exposed to high treatment than for medium, low and control treatments.* Icing will open up the canopy and allow increased amounts of light to reach the understory

beech saplings. American beech leaves in the high treatment plots will be of higher nutrient quality.

3. *Caterpillar consumption rate will be higher when fed sugar maple leaves exposed to high treatment than for medium, low and control treatments.* Caterpillars will have to eat more lower quality leaves from the canopy in order to grow the same amount.

4. *Caterpillar consumption rate will be lower when fed beech leaves exposed to high treatment than for medium, low and control treatments.* Caterpillars can eat fewer high quality leaves to grow the same amount. Increased light will increase nutrient quality of the leaves

Until recently, the majority of studies done on ice storms have been specific case studies surrounding stochastic icing events, such as the ice storm of 1998. A novel ice storm experiment at the Hubbard Brook Experimental Forest created an opportunity to study the ecological impacts of ice storms in a controlled experimental setting. This study used gypsy moth caterpillar (*Lymantria dispar* dispar) growth and consumption rates to assess leaf quality of two dominant tree species: sugar maple and American beech after an icing event.

3. Study site

The Hubbard Brook Experimental Forest (HBEF) is a 3100 ha site located in Woodstock, New Hampshire (43° 56′ N, 71° 45′ W). It is primarily a northern hardwood forest (Rustad & Campbell, 2012). Dominant species include American beech (*Fagus grandifolia*), sugar maple (*Acar saccharum*), and yellow birch (*Betula alleghaniensis*), with hemlock (*Tsuga canadensis*) at lower elevations along the Hubbard Brook, some white ash (*Fraxinus americana*) at lower and middle elevation slopes, red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera* var. *cordifolia*) at higher elevations and on rocky slopes (Rhoads et al., 2002; Driscoll et al., 2014). The ice plots are located in a 70-100 yr old mixed hardwood stand near the main branch of the Hubbard Brook (Driscoll et al., 2014). Mean annual temperature at Weather Station 1 (43° 95′ N, 71° 72′ W) is 6.82 °C (Campbell, 2014a). Mean annual precipitation is1503.39 mm (Campbell, 2014b)

4. Methods

Ice Storm Experiment

The ice storm experiment (ISE) was conducted between January 18th and February 11th, 2016. The experimental design consisted of ten 20 m by 30 m plots with an inner 10 m by 20 m plot surrounded by a 5 m buffer on all sides to minimize edge effects. The inner plot was divided into eight 5 m by 5 m subplots. Ice treatments included two control plots (no ice), two plots with 6 mm (0.25 inch) of ice, two 13 mm (0.5 inch) plots, and two 19 mm (0.75 inch) plots. Two 13 mm (0.5 inch) plots were iced again in winter 2017. Water from the nearby Hubbard Brook was used for the icing. Pilot methods for ice application were published by Rustad & Campbell (2012).

Insect species

Gypsy moth larvae (*Lymantria dispar* dispar) were used for leaf quality bioassays. The gypsy moth is a highly destructive, invasive species in North America. It is polyphagous (Liebhold et al., 1992), feeding on many species of foliage. Gypsy moths prefer to eat paper birch (*Betula papyrifera*) and red oak (*Quercus rubra*) (Houston & Valentine, 1985). Sugar maple and American beech are considered to be of intermediate quality for gypsy moth larvae (Houston & Valentine, 1985). Larvae were fed an agar-based, high protein diet in the lab. Only 3rd and 4th instar caterpillars were used.

Leaf Quality Bioassays

Foliage was collected from two to five sugar maple individuals with pole pruners at each ISE plot for a total of at least 80 leaves per plot (80 leaves/plot × 10 plots = 800 sugar maple leaves). Foliage was collected from five American beech saplings by hand at each ISE plot for a total of at least 100 leaves per plot (100 leaves/plot × 10 plots = 1000 beech leaves).

Individual gypsy moth larvae were weighed and placed in sealed tissue culture dishes with sugar maple or beech leaves (1 caterpillar/dish × 17 dishes/plot/species × 10 plots × 2 tree species = 340 replicates). Leaves were kept fresh by placing petioles in an aquatube filled with water. Dishes were placed in an incubator (25.0°C, 16 h light: 8 h dark) for approximately 72 hours. Relative growth rates (RGR) were calculated following the formula described in Ayres & Scriber (1994) and Erelli et al. (1998):

$$RGR = [\ln(M_f) - \ln(M_i)]/t$$

M_f = final larval dry mass

M_i = initial larval dry mass

t = elapsed time (days)

Relative consumption rates (RCR) were calculated using the formula in Gordon (1968):

$$RCR = 1000\ \Delta F / (We \times T)$$

ΔF = dry-weight food-intake

We = exponential mean live weight

T = elapsed time (days)

Dry masses (DM) of a random subsample of gypsy moth caterpillars were obtained in order to estimate fresh mass (FM) ($n = 30$, $DM = 0.1077 (FM) + 0.0014$).

Dry masses of a random subsample of sugar maple and American beech leaves were also obtained to estimate fresh mass (DM = 0.3838 (FM) – 0.0008 for sugar maple, DM = 0.4482 (FM) – 0.0092 for American beech). Following the 72 h incubation period, final caterpillar dry weight was obtained.

Statistical analysis

Relative growth rate and relative consumption rate were analyzed using one-way ANOVAs (α=0.05). ANOVAs were calculated using R (R Core Team, 2016).

5. Results

Relative growth rate:

Sugar maple (*Acer saccharum*)

Relative growth rate for *Lymantria dispar* dispar was greatest for the high treatment plot, and was greater than for the medium plot ($p = 0.003$), low treatment plot ($p = 0.003$), and control treatment plot ($p < 0.001$). Relative growth rate for the medium treatment plot was greater than for the control plot ($p < 0.003$), but was not different from the low treatment plot. Relative growth rate for the low plot was not different from the control plot (Figure 1).

American beech (*Fagus grandifolia*)

Relative growth rate for *Lymantria dispar* dispar was highest for the high treatment plot, and was greater than for the low plot ($p < 0.001$) and the control plot ($p < 0.001$). The high treatment plot was not different from the medium treatment plot. Relative growth rate for the medium treatment plot was greater than for the low treatment plot ($p = 0.008$). Relative growth rate for the low plot was not different from the control plot (Figure 1).

Relative consumption rate:

Sugar maple (*Acer saccharum*)

Relative consumption rate for *Lymantria dispar* dispar was lowest in the high treatment plot. Relative consumption rate was lower for the high treatment plot than for the, control treatment plot ($p = 0.010$), low treatment plot ($p = 0.012$), and the medium treatment plot ($p < 0.001$) (Figure 1).

American beech (*Fagus grandifolia*)

Relative consumption rate for *Lymantria dispar* dispar was higher for the control treatment plot than for the medium treatment plot ($p = 0.029$) and the high treatment plot ($p = 0.013$) (Figure 1).

6. Discussion

Low relative consumption rate and high relative growth rate in the high treatment plot for sugar maple indicated high leaf quality. Low relative consumption rate and high relative growth rate in the high treatment plot for beech also indicated high leaf quality. These trends could be due to increased light or nutrient availability for the leaves.

Understory sugar maple leaves are able to increase light capturing ability without increasing metabolic demand in canopy gaps (Canham, 1988). Sugar maple saplings in low gap light had higher ratios of leaf area to branch surface area and length, and therefore could capture light for photosynthesis with higher efficiency than American beech (Canham, 1988). Without an opening in the canopy, American beech will outcompete sugar maple in terms of canopy recruitment (Canham, 1988). In the high treatment plots with a large canopy gap, the sugar maple may be outcompeting American beech.

Pisaric et al. (2008) quantitatively assessed sugar maple health follow the ice storm of 1998. 86% of sugar maple trees considered to be "severely damaged" (having one or two live branches remaining) in the storm recovered within 6 years (Pisaric et al., 2008). Sugar maple is relatively resilient to ice damage as compared to other dominant hardwood species. For example, white ash (*Fraxinus americana*) declined in the years following the storm (Pisaric et al., 2008). This resilience could partially account for the trend seen with growth and consumption rates for gypsy moth larvae feeding on sugar maple leaves.

Age and light are important factors when it comes to leaf chemical defense. Murakami and Wada (1997) found that oak seedling leaves are less resistant to herbivory than adult leaves because they have a lower tannin content. Therefore, leaves from seedlings are of higher quality for herbivores than leaves from adults (Murakami & Wada, 1997). An increase in nitrogen levels as a result of extensive crown damage may account for the increase in caterpillar growth rate following high levels of ice damage. The resource availability hypothesis suggests that tree species that are not resource limited will cope with distress due to herbivory through rapid growth and leaf replacement (Bryant et al., 1983). Plant species that are resource limited do not have the capacity to respond to distress with rapid growth, and therefore allocate their resources into tissue regeneration (Bryant et al., 1983). The carbon nutrient balance hypothesis suggests that an increase in nitrogen (or any nutrient) will cause a decline in carbon-based defense hormones in plants as more resources are allocated to growth (Chapin et al., 1987). Therefore, it is possible that highly damaged trees following an ice storm are not as strongly defended as trees with less or no damage from an ice storm.

Following the ice storm of 1998, Houlton et al. (2003) found elevated levels of nitrate in the Oa leachate horizon in areas that had faced extensive crown damage as a result of ice accretion. An increase in litter input with a high carbon:nitrogen ratio likely led to an increase in soil nitrate levels at the beginning of the growing season in 1998 (Houlton et al., 2003). Over summer 1998, the compromised ability of plants to uptake nitrogen as a result of ice damage likely led to the increased levels of nitrate being leached from the soil (Houlton et al., 2003). According to the carbon nutrient balance hypothesis, the increase in nitrogen levels at the beginning of the summer may have caused a decline in plant defense hormone levels (Chapin et al., 1987). This decline would make them more susceptible to damage from insect herbivores.

Caterpillar growth rates and consumption rates indicate that leaves are higher quality or less well defended after ice storms. Chemical analyses of these leaves are currently underway, which will provide valuable insight into the mechanisms behind these patterns. Based on the results, it is expected that carbon-based defense hormones will be lowest in the high treatment plots for both the American beech and sugar maple leaves. Nitrogen levels may be higher in the high treatment plots as compared to the other treatments. Based on the findings of this study, overall leaf quality as determined by chemical content will be highest for both American beech

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Appendices

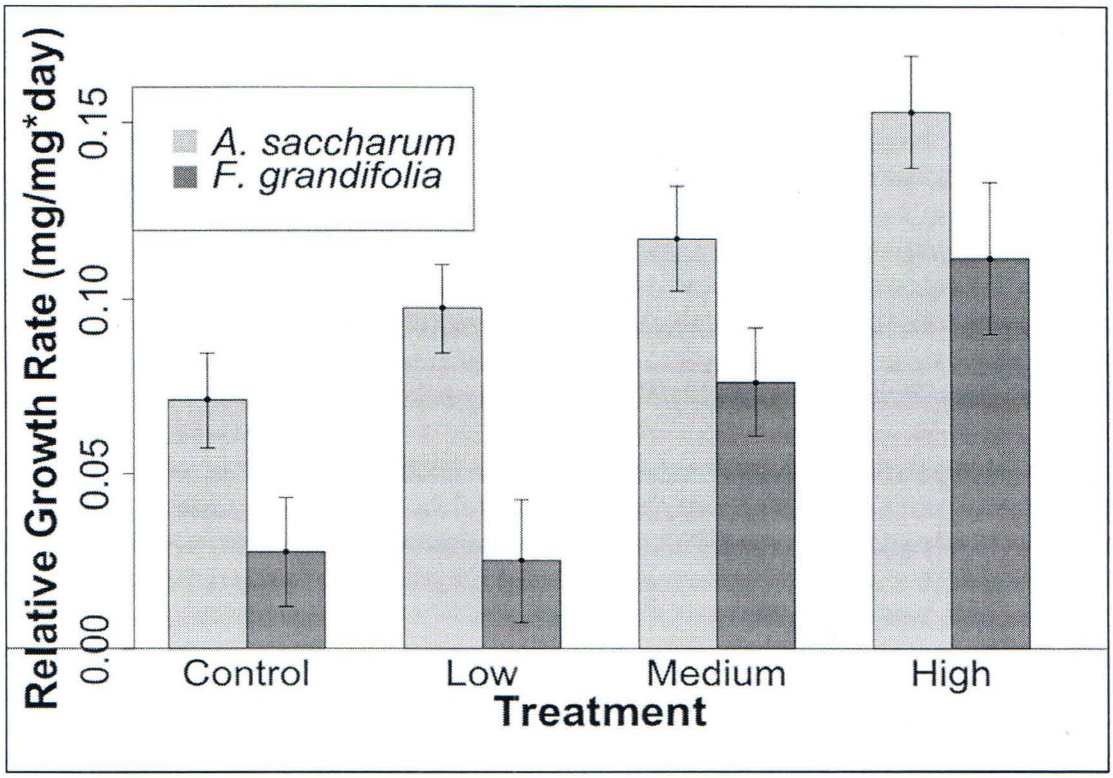

Figure 1. Relative growth rate of *Lymantria dispar* dispar when fed *Acer saccharum* and *Fagus grandifolia* foliage collected from experimental ice plots in 2016. Corresponding ANOVAs in Table 1.

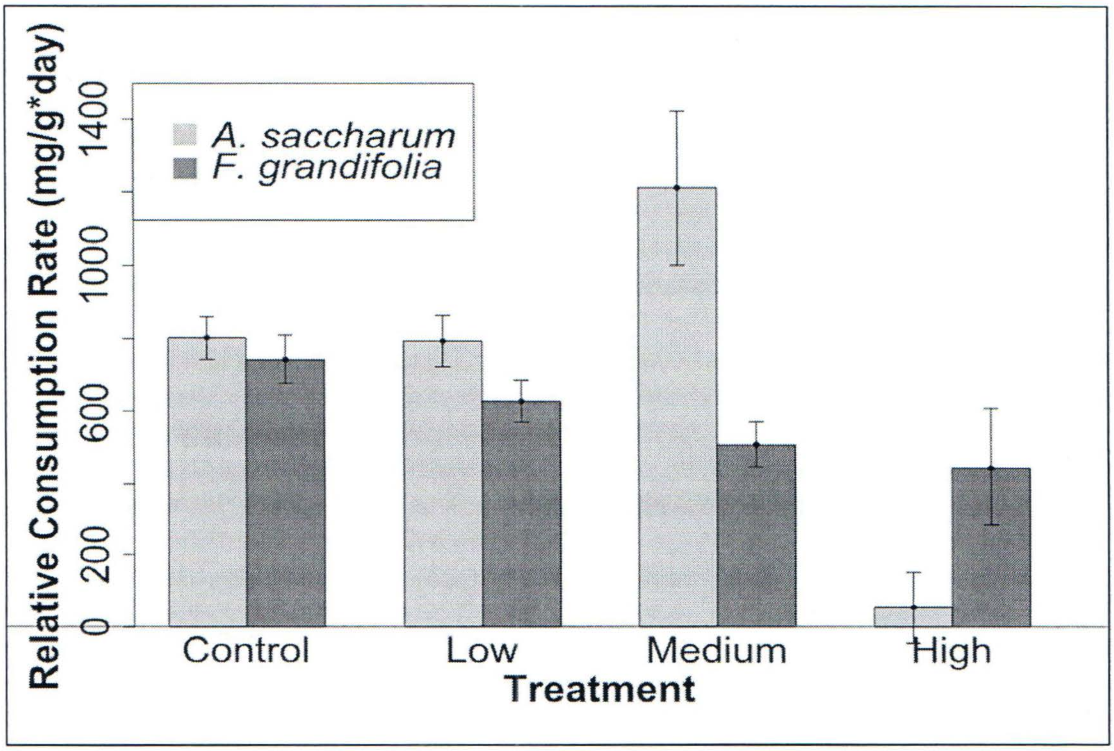

Figure 2. Relative consumption rate of *Lymantria dispar* dispar when fed *Acer saccharum* and *Fagus grandifolia* foliage collected from experimental ice plots in 2016. Corresponding ANOVAs in Table 1.

Table 1. One-way ANOVA results comparing relative growth rate and relative consumption rate of gypsy moth (*Lymantria dispar* dispar) larvae between four ice treatments, control, low, medium, and high.

Source	*df*	Sugar maple (*Acer saccharum*)		American beech (*Fagus grandifolia*)	
		F-statistic	*P-value*	*F-statistic*	*P-value*
Relative growth rate	3	10.41	<0.0001	10.81	<0.0001
Relative consumption rate	3	10.77	<0.0001	4.03	0.008